JOURNAL OF Evolutionary Biology

doi: 10.1111/jeb.13046

Reproductive trade-offs in a long-lived bird species: condition-dependent reproductive allocation maintains female survival and offspring quality

M. GRIESSER*†‡, G. F. WAGNER*†, S. M. DROBNIAK*‡ & J. EKMAN§[1]

*Department of Anthropology, University of Zurich, Zurich, Switzerland
†Institute of Ecology and Evolution, University of Bern, Bern, Switzerland
‡Institute of Environmental Sciences, Jagiellonian University, Kraków, Poland
§Department of Ecology and Genetic/Population Biology and Conservation Biology, Evolutionary Biology Centre, Uppsala University, Uppsala, Sweden

Keywords:

Brucella abortus;
intergenerational costs;
intermittent breeding;
intragenerational costs;
life history;
prebreeding condition;
reproductive costs.

Abstract

Life history theory is an essential framework to understand the evolution of reproductive allocation. It predicts that individuals of long-lived species favour their own survival over current reproduction, leading individuals to refrain from reproducing under harsh conditions. Here we test this prediction in a long-lived bird species, the Siberian jay *Perisoreus infaustus*. Long-term data revealed that females rarely refrain from breeding, but lay smaller clutches in unfavourable years. Neither offspring body size, female survival nor offspring survival until the next year was influenced by annual condition, habitat quality, clutch size, female age or female phenotype. Given that many nests failed due to nest predation, the variance in the number of fledglings was higher than the variance in the number of eggs and female survival. An experimental challenge with a novel pathogen before egg laying largely replicated these patterns in two consecutive years with contrasting conditions. Challenged females refrained from breeding only in the unfavourable year, but no downstream effects were found in either year. Taken together, these findings demonstrate that condition-dependent reproductive allocation may serve to maintain female survival and offspring quality, supporting patterns found in long-lived mammals. We discuss avenues to develop life history theory concerning strategies to offset reproductive costs.

Introduction

Life history theory is an essential framework to understand the evolution of allocation of resources into reproduction and survival (Williams, 1966; Stearns, 1992). It predicts that individuals have to trade off the allocation of their finite resources (Noordwijk & Jong, 1986), and accordingly, reproductive allocation in a given event correlates negatively with the expected lifespan of an individual (Williams, 1966; Stearns, 1992). As long-lived species invest in somatic maintenance (i.e. survival) rather than reproduction, variance in adult survival has been shown to be smaller than variance in reproductive allocation (Gaillard *et al.*, 2000; Hamel *et al.*, 2010). Consequently, their reproductive decisions are predicted to be sensitive to limitations in resource availability due to environmental stochasticity.

Field studies support the idea that long-lived species generally invest less into reproduction than short-lived species (Stearns, 1992; Hamel *et al.*, 2010; Mourocq *et al.*, 2016), and may refrain from reproduction under unfavourable conditions, that is exhibit intermittent breeding (Shaw & Levin, 2013). Intermittent breeding is most commonly reported in long-lived species that breed in temporally variable environments (Bradley *et al.*, 2000; Covas *et al.*, 2004). However, clutch or brood size manipulations, the main techniques used to

Correspondence: Michael Griesser, Department of Anthropology, University of Zurich, Winterthurerstr. 190, 8057 Zurich, Switzerland.
Tel.: +41 (0)44 635 54 23; fax: +41 44 635 68 04;
e-mail: michael.griesser@uzh.ch
[1]Deceased.

assess reproductive trade-offs in egg-laying species (Dijkstra *et al.*, 1990; Santos & Nakagawa, 2012), generally exclude individuals that exhibit intermittent breeding in the experimental season. Thus, we may systematically underestimate the extent of adjustments to reproductive allocation in long-lived species.

A number of experiments in birds did manipulate the conditions prior to breeding. They showed that food-supplemented females increase their reproductive allocation (Gasparini *et al.*, 2007; Kerr *et al.*, 2007; Karell *et al.*, 2008; Parejo *et al.*, 2012), whereas food-deprived females produce low-quality offspring (Gorman & Nager, 2004). Also, females increase clutch size, egg mass and feeding rate when predators are removed (Fontaine & Martin, 2006), but reduce clutch size under increased perceived predator abundance (Eggers *et al.*, 2006). Yet, food and predator abundance manipulations may affect multiple aspects of an individual's reproductive decisions in natural populations, calling for experiments that specifically manipulate female condition before egg laying.

Here we investigate the association between reproductive allocation, survival and offspring quantity and quality, using longitudinal and experimental data from a natural population of Siberian jays, *Perisoreus infaustus*. This open-nesting bird species is long-lived (maximum lifespan of Siberian jays = 17.9 years; average maximum lifespan of $N = 1128$ bird species: 14.4 years; Valcu *et al.*, 2014). Most females make one annual breeding attempt, laying 1–5 eggs, with re-nesting occurring in 3.1% of breeding attempts. However, they rarely refrain from breeding under unfavourable conditions (Eggers *et al.*, 2006). Previous work in the study population revealed that females adjust their reproductive allocation depending on the perceived predation risk and habitat quality, and the interplay between these two factors determines their reproductive output. Females breeding in territories with an increased risk of nest predation (Eggers *et al.*, 2006) and more open territories (Nystrand *et al.*, 2010) have smaller clutches and a lower nesting success. The principal nest predators of Siberian jays (i.e. other corvids) are visual hunters, which locate nests more easily when parents feed a larger brood (Eggers *et al.*, 2006), or when nests are located in more open habitats (Griesser *et al.*, 2007).

Siberian jays live in stable groups composed of a dominant breeding pair (hereafter referred to as breeders, or singly as female or male) and up to four non-breeders. Reproduction is strictly kept within the breeding pair (Ekman & Griesser, 2016), and in successful broods, subordinate offspring are evicted by dominant siblings within 1–2 months of fledging (Ekman *et al.*, 2002), after which they disperse to other groups to wait for a breeding opening (hereafter termed early dispersers) (Ekman *et al.* 2001, Griesser *et al.* 2014). Offspring that delay dispersal can remain with their parents up to three years (hereafter termed delayed dispersers; Griesser *et al.*, 2008), acquire territories of higher quality and have a longer lifespan and a higher lifetime reproductive success than the evicted early dispersers (Ekman *et al.* 2001, Ekman & Griesser, 2016). Because females that dispersed early have shorter lives than females that delayed their dispersal (Ekman & Griesser, 2016), they might face different reproductive trade-offs than females that delayed their dispersal, but this has not yet been tested.

We used long-term data collected over 26 years, including 20 years of detailed data on reproductive allocation, to investigate how females adjust their reproductive allocation depending on (i) annual conditions, (ii) their dispersal phenotype and (iii) breeding habitat quality. We measured reproductive allocation by females (number of eggs and fledglings) and assessed costs of reproduction by recording survival until spring of the following year for females and offspring as well as offspring body size and feather quality. As Siberian jays are a long-lived species, reproductive allocation should show high variance (high allocation in favourable years, low allocation in unfavourable years) but not affect subsequent female survival. Females that delayed their dispersal and those breeding in high-quality habitats are expected to lay larger clutches and/or bigger eggs (Noordwijk & Jong, 1986; Williams, 2001) (leading to more fledglings) than early dispersing females and those breeding in low-quality habitats. Offspring hatching from larger eggs may experience increased survival (Metcalfe & Monaghan, 2001; Krist, 2011).

To assess reproductive allocation trade-offs experimentally, we used an immune system challenge in two breeding seasons with contrasting weather conditions. We injected females with a novel antigen (*Brucella abortus* suspension; hereafter shortened to BA), a bacterium causing brucellosis in mammals. In birds, it does not occur naturally and when administered induces an immune reaction which can be detected for 2–3 weeks through the proliferation of B cells (Amat *et al.*, 2007). Injecting BA prior to breeding should change the resource allocation of females, and thus, BA-injected females were expected to i) delay the onset of breeding; ii) lay smaller clutches and/or eggs; or iii) refrain from breeding altogether, particularly in unfavourable years or when breeding in low-quality habitat. Offspring hatching from smaller eggs would be of lower phenotypic quality (Krist, 2011), leading to increased mortality during their first year of life (Metcalfe & Monaghan, 2001).

Materials and methods

We collected data for this study from an individually colour-ringed population of Siberian jays in boreal forest habitats near Arvidsjaur, Northern Sweden (65°40′ N, 19°10′ E). We used data on reproductive allocation collected between 1989 and 2014 (n = 3–55 territories

per year; increase due to enlarged study site) and experimental data collected in the years 2011 and 2012 ($n = 55$ territories). As Siberian jays are sexually monomorphic, we took 50–80 μL blood from all birds for molecular sex determination (Griffiths *et al.*, 1998). All procedures were carried out under the licence of the Umeå ethics board, licence number A 80–99, A 45–04 and A 50–11.

Assessment of reproductive allocation, offspring quality and survival

To assess reproductive allocation, we counted the number of eggs and fledglings, measured the adult body size of offspring after fledging and assessed offspring feather condition (i.e. number of fault bars, see below; Grubb, 2006). From 1989 to 2004 and from 2011 onwards, we caught females in March and attached a radio-tag (Holohil BD-2D, Telenax TBX-006), to aid with locating the nests. Nests were visited repeatedly to count the number of eggs, nestlings and fledglings, and ring all fledglings (Griesser *et al.*, 2012, Griesser *et al.* 2014). We did not follow reproduction between 2005 and 2010, but we could reliably assess whether pairs bred successfully or not (hereafter termed nesting success) based on the presence of delayed dispersing juveniles in autumn. The rank of individuals was based on dominance hierarchies among group members assessed on feeders.

To assess juvenile quality, we caught juveniles 1–3 months after fledging to measure their adult body size and count the number of fault bars in their wing and tail feathers. Fault bars are growth deficiencies visible as translucent bars across feathers, thought to reflect elevated physiological stress levels during feather growth (Grubb, 2006). An earlier study in Siberian jays showed that a high number of fault bars was linked to increased overwinter mortality of juveniles (Griesser *et al.*, 2006). Fault bars make feathers more prone to breakage, which in turn reduces manoeuvrability and escape speed during predator attacks (Williams & Swaddle, 2003). We surveyed the survival of females and delayed dispersing juveniles until the next spring by repeatedly visiting all groups in early March before the onset of the next breeding season. Earlier studies showed that all 110 individuals that were radio-tagged in autumn either remained in their territory and survived ($N = 94$), or were found dead in the territory, killed by a predator ($N = 16$; Griesser, 2013). Moreover, Siberian jay groups are very stable and nonbreeders generally only move into breeding openings in neighbour territories later on in spring (Ekman & Griesser, 2016).

Assessment of dispersal phenotype (early vs. delayed dispersing individuals)

We assessed the dispersal phenotype of individuals using two different methods: either from their life history, or using a behavioural assessment. In years that we located nests, we recognized delayed dispersing juveniles that remained on the parental territory based on their numbered metal ring. Unringed juveniles settling in groups were consequently classified as early dispersers (Griesser *et al.*, 2014). In years that we did not locate nests, we classified the dispersal phenotype of juveniles using a behavioural assessment on feeders placed in the territory in autumn, following a standardized protocol (Ekman *et al.*, 1994). Breeders are socially dominant over other group members and share a feeder with their own offspring, whereas they aggressively displace or chase unrelated group members away from a feeder (Griesser *et al.*, 2015). This method is fully reliable when compared with juveniles of known origin ($n = 120$ juveniles: all correctly assigned; Ekman *et al.*, 1994; Griesser 2003). The dispersal timing of individuals that immigrated into the study population after their first winter was unknown, and they were classified with 'unknown' dispersal phenotype.

Assessment of habitat quality

The study site has two areas, one dominated by managed forests and the other by unmanaged forests (Griesser *et al.*, 2007). The managed area is located closer to human settlements and has a higher number of nest predators compared to the unmanaged area (Eggers *et al.*, 2005). In addition, forests in managed territories are more open, and consequently, adult birds have a higher risk of being killed by their main predators, accipiter hawks (goshawk *Accipiter gentilis,* sparrowhawk *A. nisus*), than birds living in unmanaged territories (Griesser *et al.*, 2006).

Immunological challenge experiment

We performed an immunological challenge experiment in two breeding seasons with different weather conditions. In 2011, mean spring temperatures (April, May) were 2.7°C warmer than the long-term average and the mean nesting success was the highest (83%) since the onset of fieldwork in our study population in 1989. In 2012, the mean spring temperatures were 0.3°C below average and the mean nesting success (29%; excluding BA-injected females) was lower than average (42%). We used a counterbalanced design to assign females with known dispersal phenotype ($n = 27$) to a treatment group (sum over both years: BA: $n = 20$, saline: $n = 21$), balancing habitat quality (managed, unmanaged forests) and the weighted average of the long-term mean nesting success of the territory relative to all other territories (see Griesser *et al.*, 2007 for detailed description of calculation). We also injected four females of unknown phenotype. Most females of unknown phenotype ($n = 22$), along with 5

delayed dispersing females and 5 early dispersing females, were not injected (labelled control hereafter) to have baseline data available for untreated birds (Table S1). For females which were injected in both years, we used the reverse treatment in 2012 ($n = 15$). We note that the experimental treatment in the first year did not influence the reproductive investment and female survival in the second year (Table S2).

We captured females in March, 13–49 days (mean ± SE: 29.3 ± 2.2 days) before the onset of egg laying (mean long-term onset of egg laying: 6th April) using mist nets or ground nets, attached a radio-tag and injected 100 μL BA solution (Veterinary Laboratories Agency, Addlestone, UK) or 100 μL sterile saline solution intraperitoneally, or did not inject anything (controls). The dosage was chosen carefully based on several earlier studies injecting BA solution in birds (Birkhead *et al.*, 1998; Amat *et al.*, 2007; Sild *et al.*, 2011). We chose this time window to ensure that females experienced the effect of the BA injection before the onset of egg laying. We followed females regularly with the help of the radio-tags, until we found their nest. We were unable to locate nests in nine cases, either due to predation of the female ($n = 2$) or male ($n = 1$; females without males do not nest), or due to radio-tag failure ($n = 6$). Once temperatures were warm enough (>5°C), we returned to climb the nest tree to count the number of eggs and measure them with dial callipers (0.1 mm accuracy). Nests were visited 2–5 times during the nestling period to measure the nestlings and to ring them with a numbered metal ring and three colour rings. We applied clip marks to claws to identify individual nestlings before ringing.

Statistical analyses

We used ASReml v. 3.0 (Gilmour *et al.*, 2009) in R 3.0.2 (Team, 2014) to run linear mixed models (LMM) and generalized linear mixed models (GLMM). The decision whether to use LMM or GLMM was based on the inspection of residuals on diagnostic plots, except for binary data, where in all cases binomial error GLMMs were used.

Long-term data

We tested with a random regression LMM whether annual condition (assessed as the mean proportion of females that fledged at least one offspring in the population), habitat quality, female age and female phenotype affected the number of eggs individual females laid across different years. Defining annual condition in a measurement that integrates the fitness consequences for the organism (e.g. using breeding success as here, or offspring survival as in a study on Soay sheep *Ovis aries* (Robinson *et al.*, 2009)) has been suggested to lead to a composite measure of poor and good annual conditions in a relevant 'currency' (Stinchcombe & Kirkpatrick, 2012). Intuitively, average clutch size and the proportion of successfully breeding females in a population could be closely linked due to a statistical artefact. We excluded this possibility using a simple simulation based on the breeding parameters observed in our study population (see Data S1). The average clutch size and annual mean nesting success could be correlated when nests with a small clutch size are more likely to fail than nests with a larger clutch size. Given that females do not initiate a clutch only in exceptional cases, we excluded these cases from the simulation. The simulation showed that the correlation between the two quantities cannot arise due to statistical sampling and mathematical artefacts, supporting the biological value of the mean annual nesting success.

We excluded nests of females that were experimentally challenged with BA in 2012, nests of females that were exposed to predator playbacks (Eggers *et al.*, 2006) and females that lacked a mate. We included female identity as a random factor to control for the repeated use of the same females in subsequent years. Random slopes enabled additional variation in the steepness of relationships between reproductive allocation and annual condition across individual females. We used the same type of model and independent variables to investigate the influence of annual condition on the number of fledglings. We used GLMMs (binomial error structure, logit link function) to assess the influence of whether females bred successfully or not, number of eggs, habitat quality, female age and female phenotype on female survival until the following year, including territory and year as random factors.

To assess offspring adult body size and feather quality, we first ran principal component analyses to reduce bivariate, co-linear data into single variables. Given that a higher number of fault bars corresponds to low feather quality, we multiplied the number of fault bars by -1, so that a higher number corresponds to high feather quality. The PCA for body size included tarsus length and wing length; the PCA for feather quality included the maximum numbers of fault bars in wing and tail feathers. In both PCAs, the first PC, respectively, explained 77% and 71% of the variance, and thus, only the first PCs were used as response variables in subsequent models (Table S3). We analysed these data using LMMs including annual condition, female age and phenotype, habitat quality and the number of siblings on offspring feather quality and offspring adult body size, including territory and year as random factors.

We investigated whether the mean-standardized measures of within-year variance (coefficients of variation, calculated from raw data) in reproductive and quality traits of individuals differed. We used a Kruskal–Wallis test due to lack of both normality and homogeneity of variance between different types of

traits. Variances were calculated assuming appropriate distribution of the original data. For the number of eggs and fledglings, we assumed Poisson distribution, and thus *variance = mean*, and for female and offspring survival, we assumed binomial distribution, and thus *variance = mean*(1–mean)*.

Experimental data

Data on reproductive allocation of females were analysed using general linear mixed models in a repeated measures framework. We included female investment as a response variable in the model, measured as the number of eggs, nestlings and fledglings at the respective stage of the breeding cycle. Accordingly, the investment was treated as a repeated measure and the repetition level was the stage of the cycle, included in the model as a fixed categorical variable. We included the following fixed effects in the model: experimental treatment (categorical variable: BA/saline/control), year (categorical variable: 2011/2012), habitat quality (categorical variable: managed/unmanaged forest), female phenotype (categorical variable: kin/nonkin/unknown), female age (continuous) and the time difference between BA injection and egg laying for each female (continuous variable). To account for possible repeated measurements of individuals ($N = 27$ females were studied in both years), we included female identity as a random categorical variable. In our framework, estimates of the stage variable provide a means to assess the change in female investment over the course of the reproductive cycle, and its interaction with treatment shows how much the rates of these changes vary across the experimental groups.

We investigated the association between our treatment and whether females initiated a clutch or not, or abandoned their brood or not, with Fisher's exact tests. We tested for differences in the volume of individual eggs (calculated following Hoyt, 1979) using a LMM, including nest identity as a random factor. We tested the influence of the treatment on offspring adult body size and feather quality using a LMM ($n = 83$ offspring), while female survival until the next year, and survival of delayed dispersing juveniles until the next year ($n = 83$ offspring) were analysed using GLMMs (binomial error structure, logit link function). In all models testing offspring parameters, we included female identity as random factor to control for the fact that we sampled several offspring of the same female.

We included the following measurements as independent variables in all models assessing experimental data: injection treatment (BA, saline, control), number of days between catching the females to inject them (or not in case of the control females) and median egg-laying date of the year, habitat quality (managed vs. unmanaged), year (2011 vs. 2012) and female phenotype (early disperser, delayed disperser, unknown). We used the median egg-laying date instead of the actual egg-laying date given that in 2012 most BA-injected females did not attempt to breed. In models assessing offspring size, quality and survival, we also included the number of siblings in the models.

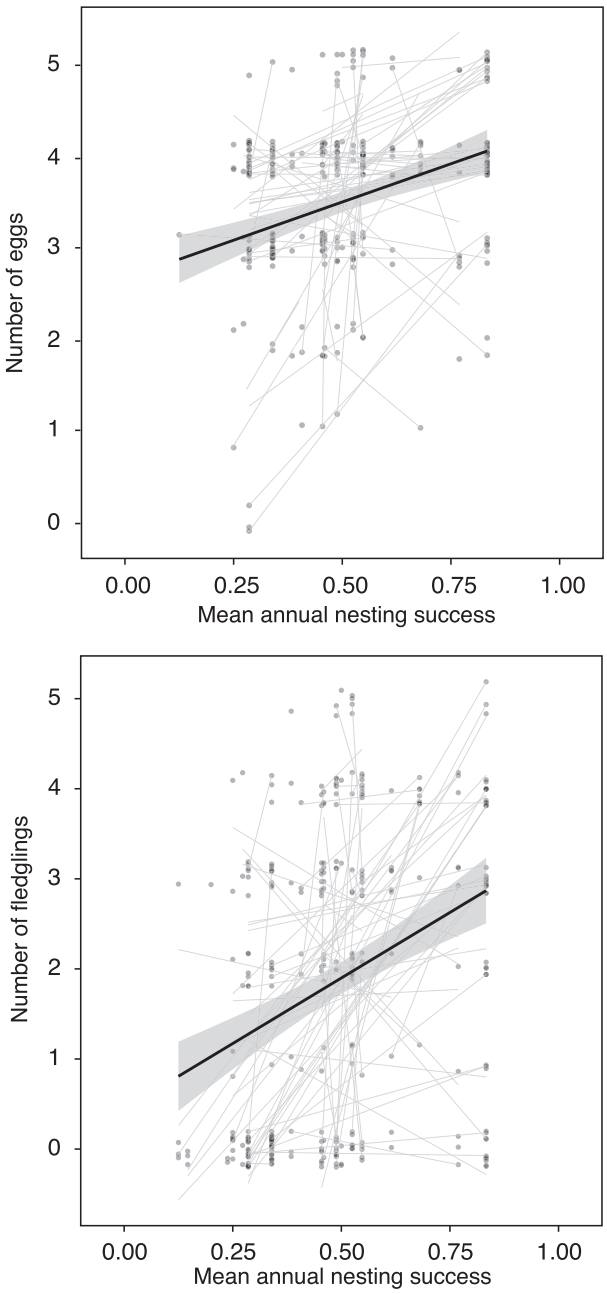

Fig. 1 Individual changes in number of eggs (a) and number of fledglings (b) depending on mean annual nesting success. Grey lines: regression slopes for individual females; black line: population-level slope (with its 95% credibility interval indicated by the grey area), for number of eggs: marginal regression slope = 1.47, $P < 0.001$, for number of fledglings: marginal regression slope = 2.94, $P < 0.001$. For clarity, the original data points are jittered around their exact values along the y-axis to make overlapping points visible.

Results

Long-term data

The annual mean number of eggs varied between 0.75 and 3.98 across years (mean ± SE = 3.29 ± 0.19) and was higher in years with a high mean nesting success (i.e. a high proportion of successful broods) than in years with a low mean annual nesting success (Fig. 1a, Table 1a). Of 328 surveyed breeding attempts (N = 166 females), females did not initiate a clutch and skipped breeding only in five attempts, and these events were associated with adverse weather conditions during spring in 1997 (n = 2), an experimental increase in the perceived nest predation risk (n = 2, excluded from the statistical analyses; Eggers *et al.*, 2006), or low female condition (n = 1). Also, older females and those breeding in unmanaged habitat laid larger clutches than younger females and those breeding in managed habitat (Table 1a). A lower number of eggs *per se* did not lead to a lower nesting success, as partial nest predation was rare (n = 1 of 66 depredated nests) and all nests with infertile eggs also contained fertile eggs that hatched (n = 76 nests). Rather, nests were either successful (n = 209) or they failed due to nest predation (n = 66), predation of a breeder (n = 7), were abandoned (n = 12), or the nest failure reason could not be determined (n = 34). The annual mean number of fledglings varied between 0 and 3.60 across years (mean ± SE = 1.75 ± 0.09; Fig. 1b), and more nestlings fledged in favourable years than unfavourable years (Table 1b).

In favourable years (i.e. with a high mean nesting success), offspring had a higher feather quality than in years with a low mean nesting success, and offspring of older females and those from larger broods had lower feather quality (n = 249 offspring; Table 1c). However, adult body size of offspring did not vary across years (n = 332 offspring; Table 1d; Fig. 2), and no factor was found to influence survival of delayed dispersing offspring until the next spring (n = 360 offspring; Table 1e). Older females had a lower survival until the next spring than younger females, but no other factor was found to influence female survival (n = 243 females, 758 observations; Table 1f).

The variance of the number of fledglings was larger than the variance of the number of eggs and the survival of females until the next year, but did not differ among the other factors (Fig. 3; pairwise Kruskal–Wallis corrected for multiple comparisons; no. of fledglings vs. no. of eggs: P = 0.0002, no. of fledglings vs. female survival: P = 0.0004, all other comparisons: P > 0.10).

Immunological challenge experiment

The onset of egg laying was earlier in the favourable year (2011) than in the unfavourable year (2012) (GLMM: Wald test $_{\text{d.f.}\,=\,1}$ = 166.0, P < 0.00001), but did not differ between BA- and saline-injected females (GLMM: Wald test $_{\text{d.f.}\,=\,2}$ = 1.1, P = 0.33). The time span between catching a female and the median annual laying date was controlled for and did not influence the conclusions regarding experimental effects (Table 2a–c). BA injections were only associated with a lower number of eggs in 2012 (Figs 4–5; Table 2a), when five of 12 BA-injected females did not initiate a clutch (Fig. 4; Fisher exact test combining both years: P = 0.0012), and another three BA-injected females abandoned their nest during the egg stage (Fig. 4). Thus, BA-injected females laid fewer eggs than

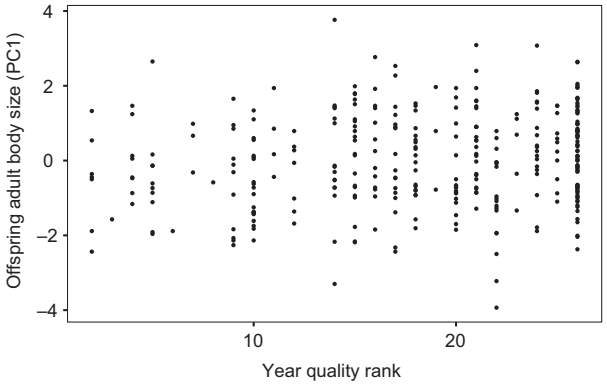

Fig. 2 Variation in offspring adult body size across years (1989–2013), ordered according to quality of the year (i.e. the mean nesting success in the study population). Adult body size of offspring was independent of mean annual nesting success (see Table 1).

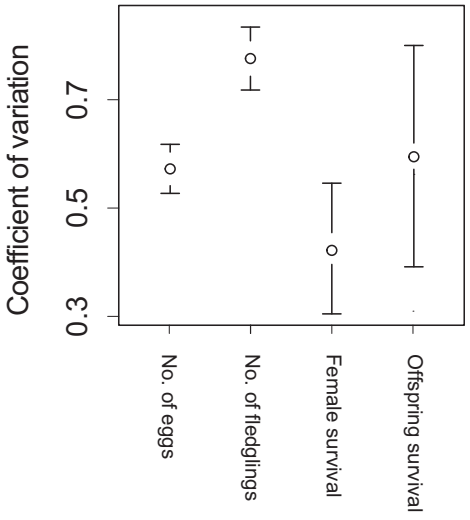

Fig. 3 Mean-standardized measures of within-year variance (expressed as coefficients of variation) of the number of eggs, the number of fledglings, female survival and offspring survival across all years. The variance of the number of fledglings is significantly higher than for the number of eggs and female survival.

Table 1 Linear mixed models and generalized linear mixed models investigating the factors affecting the number of eggs (a) and fledglings (b), offspring feather quality (c) and body size (d), and female and offspring survival until next year (e and f) in Siberian jays using longitudinal data. The factor 'nest failure reason' was included to control for the number of eggs and fledglings independent of nest failure. Significant factors highlighted in bold. den. d.f.: denominator degree of freedom; *F*: conditional *F*-statistic; effect sizes: estimates from linear models, for categorical variables expressed as contrasts with the reference category (i.e. treatment contrasts in *R*); *Z* ratio = effect size/SE. Early: early dispersed females, delayed: delayed dispersed females, unkn: unknown female dispersal phenotype, man: managed habitat, unman: unmanaged habitat, suc: successful reproduction, pred: nest depredated, other: other reason of nest failure.

Model Factor	d.f.	den. d.f.	*F*	*P*	Effect size levels of categorical variables	Solution	SE	*Z* ratio
(a) Number of eggs								
Intercept	1	143.60	3650	**<0.00001**		**2.37**	**0.23**	**10.28**
Female age	**1**	**240.50**	**9.83**	**0.0009**		**0.08**	**0.02**	**3.36**
Female dispersal phenotype	2	130.10	0.12	0.68	Imm vs. delayed	0.05	0.19	0.24
					Imm vs. unknown	−0.09	0.14	−0.63
Annual condition	**1**	**81.00**	**24.75**	**0.00001**		**1.49**	**0.32**	**4.61**
Habitat	**1**	**121.50**	**4.64**	**0.032**	Man vs. unman	**0.29**	**0.13**	**2.16**
Nest failure reason	1	233.80	0.81	0.37	Suc vs. failed	0.11	0.12	0.90
(b) Number of fledglings								
Intercept	1	61.4	1.76	0.19		−0.01	0.37	−0.02
Female age	1	74.5	0.80	0.37		0.03	0.04	0.77
Female dispersal phenotype	2	99.9	1.65	0.20	Early vs. delayed	0.62	0.30	2.03
					Early vs. unknown	0.30	0.22	1.40
Annual condition	**1**	**76.9**	**33.56**	**<0.00001**		**3.23**	**0.54**	**5.97**
Habitat	1	100.30	0.22	0.64	Man vs. unman	−0.05	0.21	−0.22
(c) Offspring feather quality								
Intercept	**1**	**69**	**8.85**	**0.004**		**1.72**	**0.66**	**2.59**
Female age	**1**	**69**	**5.54**	**0.02**		**0.12**	**0.05**	**2.35**
Female dispersal phenotype	2	69	0.11	0.90	Delayed vs. early	−0.13	0.34	−0.39
					Delayed vs. unknown	−0.02	0.32	−0.07
Annual condition	**1**	**69**	**27.46**	**<0.00001**		**−3.42**	**0.65**	**−5.24**
Habitat	1	69	0.008	0.93	Man vs. unman	-0.02	0.25	−0.09
Number of siblings	**1**	**69**	**7.01**	**0.01**		**0.33**	**0.12**	**2.65**
(d) Offspring body size								
Intercept	**1**	**44.1**	**4.36**	**0.04**		**−1.81**	**0.80**	**−2.26**
Female age	1	44.4	0.94	0.34		0.06	0.06	0.97
Female dispersal phenotype	2	57.3	2.62	0.08	Delayed vs. early	**0.86**	**0.40**	**2.16**
					Delayed vs. unknown	0.34	0.39	0.87
Annual condition	1	67.6	3.26	0.08		1.37	0.76	1.80
Habitat	1	32.1	0.07	0.79	Man vs. unman	−0.08	0.29	−0.27
Number of siblings	1	41.3	0.12	0.72		0.05	0.15	0.35
(e) Offspring survival								
Intercept	1	37.1	2.16	0.15		1.72	1.50	1.15
Female age	1	32.7	0.39	0.54		−0.06	0.10	−0.62
Female dispersal phenotype	2	49.3	0.06	0.94	Delayed vs. early	−0.04	0.70	−0.06
					Delayed vs. unknown	0.16	0.71	0.23
Annual condition	1	76	0.13	0.72		−0.52	1.45	−0.36
Habitat	1	25.7	0.27	0.61	Man vs. unman	0.27	0.52	0.52
Number of siblings	1	33.8	0.22	0.64		−0.13	0.27	−0.46
(f) Female survival								
Intercept	**1**	**304.00**	**81.82**	**0.0002**		**2.00**	**0.60**	**3.34**
Female age	**1**	**159.50**	**4.46**	**0.019**		**−0.15**	**0.06**	**−2.36**
Female dispersal phenotype	2	92.50	1.29	0.27	Early vs. unknown	0.15	0.32	0.46
					Early vs. delayed	0.84	0.52	1.62
Annual condition	1	304.00	0.02	0.63		−0.39	0.82	−0.48
Habitat	1	86.30	0.49	0.46	Man vs. unman	0.25	0.34	0.75
Nesting success	1	304.00	1.31	0.25	Succ vs. failed	−0.36	0.31	−1.14

Table 2 Linear mixed models (LMM) and generalized linear mixed models (GLMM) investigating the influence of an experiment that immunologically challenged Siberian jay females ahead of egg laying with *Brucella abortus*, saline solution or no treatment. Models assessed the influence of the experimental treatment and year (2011: favourable year, 2012: unfavourable year) on reproductive allocation (number of eggs, nestlings, fledglings; a), reproductive allocation excluding nest that failed due to nest predation (b), egg volume (c), offspring body size (d) and feather quality (e), and female and offspring survival until the next year (f and g). Significant factors highlighted in bold. den. d.f.: denominator degree of freedom; *F*: conditional *F*-statistic; effect sizes: estimates from linear models, for categorical variables expressed as contrasts with the reference category (i.e. treatment contrasts in *R*); *Z* ratio = effect size/SE. Early: early dispersed females, delayed: delayed dispersed females, unkn: unknown female dispersal phenotype, man: managed habitat, unman: unmanaged habitat, BA: Burcella abortus-injected females, con: control females, sal: saline-injected females, stage: phrase of reproductive stage: egg, nestling, fledgling stage. Random part of the repeated measurement regression of model a is shown in Table S4.

Model: Factor	d.f.	den. d.f.	*F*	*P*	Effect size levels (categorical variables)	Solution	SE	*Z* ratio
(a) reproductive allocation								
Intercept	**1**	**202.0**	**900.90**	**<0.00001**		0.10	0.55	0.18
Treatment	2	**202.0**	**2.38**	**0.040**	BA vs. cont	−0.14	0.18	−0.79
					BA vs. sal	−0.06	0.19	−0.33
Year	**1**	**202.0**	**15.13**	**<0.00001**	2011 vs. 2012	**−1.47**	**0.23**	**−6.40**
Habitat	1	202.0	2.08	0.06	Managed vs. natural	0.17	0.09	1.88
Stage	**2**	**202.0**	**8.38**	**0.0006**	Eggs vs. nestl.	−0.42	0.22	−1.93
					Eggs vs. fledglings	**−0.51**	**0.22**	**−2.28**
Female phenotype	2	202.0	0.99	0.06	Delayed vs. early	0.08	0.12	0.66
					Delayed vs. unkn	**0.29**	**0.13**	**2.25**
Female age	1	202.0	3.05	0.40		0.01	0.02	0.85
Timing injection	**1**	**202.0**	**12.37**	**0.011**		**0.03**	**0.01**	**2.55**
Treatment × year	**2**	**202.0**	**6.82**	**0.001**	BA vs. cont × 2011 vs. 2012	**0.84**	**0.25**	**3.33**
					BA vs. sal × 2011 vs. 2012	**0.93**	**0.27**	**3.51**
Treatment × stage	4	202.0	0.29	0.89	BA vs. cont × eggs vs. nestl.	0.20	0.25	0.82
					BA vs. sal × eggs vs. nestl.	0.10	0.28	0.38
					BA vs. cont × eggs vs. fledg.	0.23	0.26	0.90
					BA vs. sal × eggs vs. fledg.	0.17	0.29	0.61
(b) reproductive allocation excluding nest that failed due to nest predation:								
Intercept	**1**	**176.0**	**755.10**	**<0.00001**		0.06	0.59	0.10
Treatment	**2**	**176.0**	**1.50**	**0.046**	BA vs. cont	−0.09	0.20	−0.44
					BA vs. sal	0.01	0.21	0.04
Year	**1**	**176.0**	**19.61**	**<0.00001**	2011 vs. 2012	**−1.85**	**0.28**	**−6.65**
Habitat	1	176.0	0.34	0.32	Man vs. unman	0.10	0.10	1.01
Stage	**2**	**176.0**	**5.20**	**0.006**	Eggs vs. nestl.	−0.30	0.23	−1.27
					Eggs vs. fledglings	−0.36	0.24	−1.51
Female phenotype	**2**	**176.0**	**1.13**	**0.044**	Delayed vs. early	0.12	0.12	0.99
					Early vs. unkn	**0.34**	**0.14**	**2.45**
Female age	1	176.0	5.52	0.23		0.02	0.02	1.22
Timing injection	**1**	**176.0**	**9.48**	**0.026**		**0.03**	**0.01**	**2.24**
Treatment × year	**2**	**176.0**	**9.29**	**0.0001**	BA vs. cont × 2011 vs. 2012	**1.18**	**0.32**	**3.73**
					BA vs. sal × 2011 vs. 2012	**1.30**	**0.31**	**4.17**
Treatment × stage	4	176.0	0.09	0.99	BA vs. cont × eggs vs. nestl.	0.10	0.27	0.35
					BA vs. cont × eggs vs. fledg.	0.10	0.28	0.38
					BA vs. sal × eggs vs. nestl.	−0.02	0.30	−0.05
					BA vs. sal × eggs vs. fledg.	0.03	0.30	0.10
(c) egg volume								
Intercept	**1**	**149.5**	**551.6**	**0.00001**		**6546.84**	**377.81**	**17.33**
Treatment	**2**	**185.8**	**7.23**	**0.0009**	BA vs. cont	165.66	139.47	1.19
					BA vs. sal	**−344.59**	**169.10**	**−2.04**
Year	**1**	**167.5**	**13.85**	**0.0003**	2011 vs. 2012	**−895.72**	**183.69**	**−4.88**
Habitat	1	44.2	2.32	0.14	Man vs. unman	177.98	116.90	1.52
Female phenotype	2	48.5	0.40	0.67	Delayed vs. early	103.79	154.37	0.67
					Early vs. unkn	−9.43	158.40	−0.06
Clutch size	1	161.8	0.92	0.34		61.81	64.51	0.96
Female age	**1**	**45.9**	**7.00**	**0.01**		**59.65**	**22.54**	**2.65**
Timing injection	1	99.2	0.83	0.36		6.28	6.90	0.91
Treatment × year	**2**	**112.9**	**7.40**	**0.001**	BA vs. cont × 2011 vs. 2012	**592**	**186.54**	**3.17**
					BA vs. sal × 2011 vs. 2012	**1165.15**	**302.31**	**3.85**

Table 2 (*Continued*)

Model: Factor	d.f.	den. d.f.	*F*	*P*	Effect size levels (categorical variables)	Solution	SE	*Z* ratio
(d) offspring body size								
Intercept	1	29.1	0.48	0.49		−1.88	1.04	−1.81
Treatment	2	47.5	1.59	0.21	BA vs. cont	0.67	0.36	1.87
					BA vs. sal	0.35	0.45	0.78
Year	**1**	**53.6**	**5.89**	**0.02**	2011 vs. 2012	**−1.42**	**0.63**	**−2.27**
Habitat	1	32.1	0.14	0.71	Man vs. unman	−0.12	0.31	−0.37
Female phenotype	2	31.9	1.08	0.35	Delayed vs. early	0.46	0.38	1.22
					Early vs. unkn	−0.01	0.38	−0.02
Female age	**1**	**29.6**	**4.97**	**0.04**		**0.13**	**0.06**	**2.23**
Number of siblings	1	30.4	0.28	0.60		0.08	0.15	0.53
Timing injection	1	30.5	0.43	0.52		0.01	0.02	0.65
Treatment × year	1	64.3	0.54	0.47	Cont vs. sal × 2011 vs. 2012	0.70	0.95	0.73
(e) offspring feather quality								
Intercept	**1**	**69.0**	**6.54**	**0.01**		−1.15	1.16	−0.99
Treatment	2	69.0	1.07	0.35	BA vs. cont	−0.14	0.41	−0.34
					BA vs. sal	−0.15	0.51	−0.29
Year	**1**	**69.0**	**30.95**	**0.00001**	2011 vs. 2012	**4.48**	**0.71**	**6.30**
Habitat	1	69.0	0.36	0.55	Man vs. unman	0.21	0.35	0.60
Female phenotype	2	69.0	0.64	0.53	Delayed vs. early	0.44	0.42	1.06
					Early vs. unkn	0.10	0.42	0.23
Female age	1	69.0	2.03	0.16		0.09	0.06	1.42
Number of siblings	**1**	**69.0**	**5.29**	**0.02**		**0.39**	**0.17**	**2.30**
Timing injection	1	69.0	1.00	0.32		−0.02	0.02	−1.00
Treatment × year	**1**	**69.0**	**10.75**	**0.002**	Cont vs. sal × 2011 vs. 2012	**−3.58**	**1.09**	**−3.28**
(f) offspring survival								
Intercept	1	30.6	1.16	0.29		−2.01	2.08	−0.97
Treatment	2	48.9	0.02	0.98	BA vs. sal	0.15	0.7	0.21
					BA vs. cont	0.07	0.88	0.08
Year	1	73.0	0.13	0.72	2011 vs. 2012	−0.31	1.14	−0.28
Habitat	1	29.9	0.04	0.85	Man vs. unman	−0.11	0.58	−0.20
Female phenotype	2	28.1	0.04	0.96	Delayed vs. unkn	0.10	0.73	0.13
					Delayed vs. early	−0.11	0.73	−0.14
Number of siblings	1	32.4	0.31	0.58		0.16	0.3	0.56
Timing injection	1	30.6	0.16	0.70		0.02	0.04	0.40
Treatment × year	1	73.0	0.00	0.99	Cont vs. sal × 2011 vs. 2012	−0.03	1.87	−0.02
(g) female survival								
Intercept	1	72.7	0.32	0.58		−4.21	8.73	−0.48
Treatment	2	84.8	0.59	0.56	BA vs. sal	1.13	2.63	0.43
					BA vs. cont	−1.00	2.23	−0.45
Year	1	45.2	0.69	0.41	2011 vs. 2012	−2.10	3.82	−0.55
Habitat	1	43.7	0.99	0.33	Man vs. unman	1.76	1.77	0.99
Female phenotype	2	38.3	0.34	0.71	Delayed vs. unkn	−1.82	2.49	−0.73
					Delayed vs. early	−2.40	2.99	−0.80
Female age	1	30.7	1.94	0.17		−0.40	0.29	−1.39
Number of fledglings	1	80.7	1.24	0.27		0.80	0.71	1.11
Timing injection	1	41.4	0.99	0.33		0.19	0.19	0.99
Treatment × year	2	96.0	0.04	0.96	BA vs. cont × 2011 vs. 2012	−0.44	4.36	−0.10
					BA vs. sal × 2011 vs. 2012	7.40	28.83	0.26

saline-injected or untreated females (Figs 4–5, Table 2a). The volume of individual eggs was significantly larger in 2011 than in 2012, and BA-injected females laid smaller eggs than saline-injected females (Fig. 5, Table 2c). Accordingly, the total number of nestlings and fledglings was higher in 2011 than in 2012, and BA-injected females had fewer nestlings and fledglings (Figs 4–5). The lower number of nestlings and fledglings of BA-injected females was not a consequence of increased nest predation rates, which did not differ between the treatment groups (Fishers exact test $P = 0.30$; Table 2b).

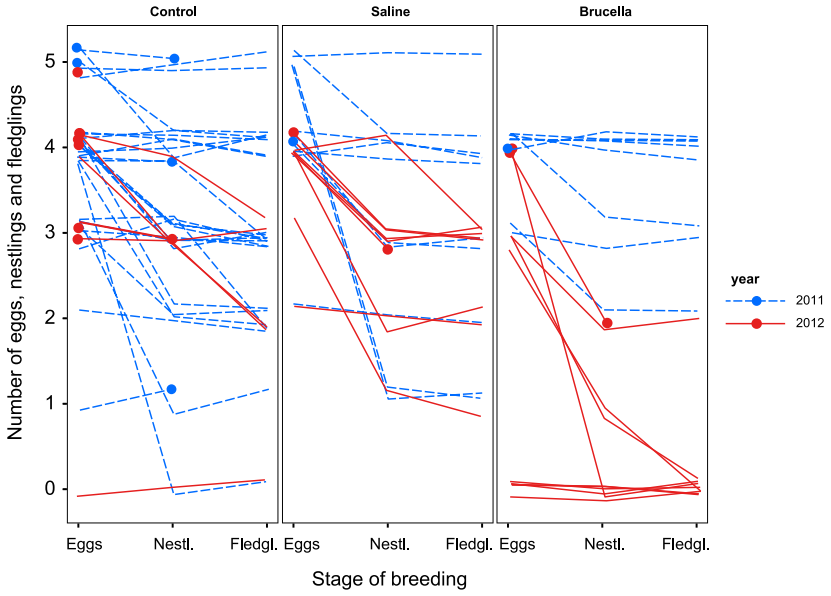

Fig. 4 Change in reproductive allocation (number of eggs, nestlings, fledglings) in the three treatment groups (*Brucella abortus*: dotted lines, saline: dashed lines, control: solid lines), split by year (2011: favourable year, 2012: unfavourable year). In nests which failed due to predation, the last measurement is marked with a circle. The nesting success was much higher in 2011 than in 2012, and treatment groups showed no difference in reproductive allocation. In 2012, *Brucella abortus*-injected females had a much lower allocation (five females did not initiate a nest; three females abandoned the nest). One control female did not imitate a nest in 2012 since her male died before egg laying. For clarity, the values are jittered around the exact numbers on the y-axis to make overlapping lines visible.

Most BA-injected females elected to skip breeding or abandoned their clutch soon after egg laying in 2012. Thus, it was not possible to assess the effect of BA injections on the full-grown body size of offspring and their condition under unfavourable conditions. In 2011, no factor was associated with full-grown body size (Fig. 5, Table 2d). In 2012, feather quality correlated negatively with the number of siblings in the brood (Fig. 5, Table 2e), yet survival of delayed dispersing offspring until the following spring was not affected by any factor (n = 83 offspring; Fig. 5, Table 2f). BA-injected females did not differ in their survival until the following spring compared to saline-injected or untreated females (Fig. 5, Table 2g).

Discussion

Our results show that reproductive allocation in the Siberian jay, a long-lived bird species, depends on both annual conditions and female body condition. Long-term data revealed that females reduce the number of eggs in bad years with a high risk of reproductive failure (Fig. 1), but rarely refrain from breeding. Accordingly, females produce fewer fledglings in bad years, but neither the annual conditions nor the number of fledglings affect female survival, first-year offspring survival or offspring body size (Table 1). Thus, the number of eggs and female survival both had a lower variance than the number of fledglings, reflecting that a substantial proportion of nests failed (Fig. 3). An experimental challenge with a novel pathogen replicated these patterns. Females with an experimentally reduced body condition elected to skip breeding only in a bad year, but we did not detect any downstream effects. Thus, condition-dependent reproductive allocation acts to keep costs of reproduction in a long-lived species constant, casting new light on the evolution of reproductive trade-offs in birds.

In a number of species, individuals reduce their reproductive investment (even to the point of refraining from breeding altogether) under harsh environmental conditions (Grant *et al.*, 2000; Cubaynes *et al.*, 2010; Pardo *et al.*, 2014) and/or when in low body condition (Clutton-Brock, 1991; Roff, 1992; Erikstad *et al.*, 1998). Our experimental challenge with BA demonstrated that the joint occurrence of harsh environmental conditions and reduced body condition lead to a reduced reproductive allocation, but not to any detectable downstream effect (Fig. 2, 4–5, Table 2). Thus, this is the first experimental study confirming that long-lived species indeed reduce their reproductive allocation under harsh environmental or low body conditions, even leading to intermittent breeding (Shaw & Levin, 2013). In contrast to nests of untreated females that usually fail late in the nestling stage due to predation, most BA-injected females that laid eggs abandoned them early on in incubation or soon after hatching (Fig. 4). Thus, BA-injected females seemed to reduce

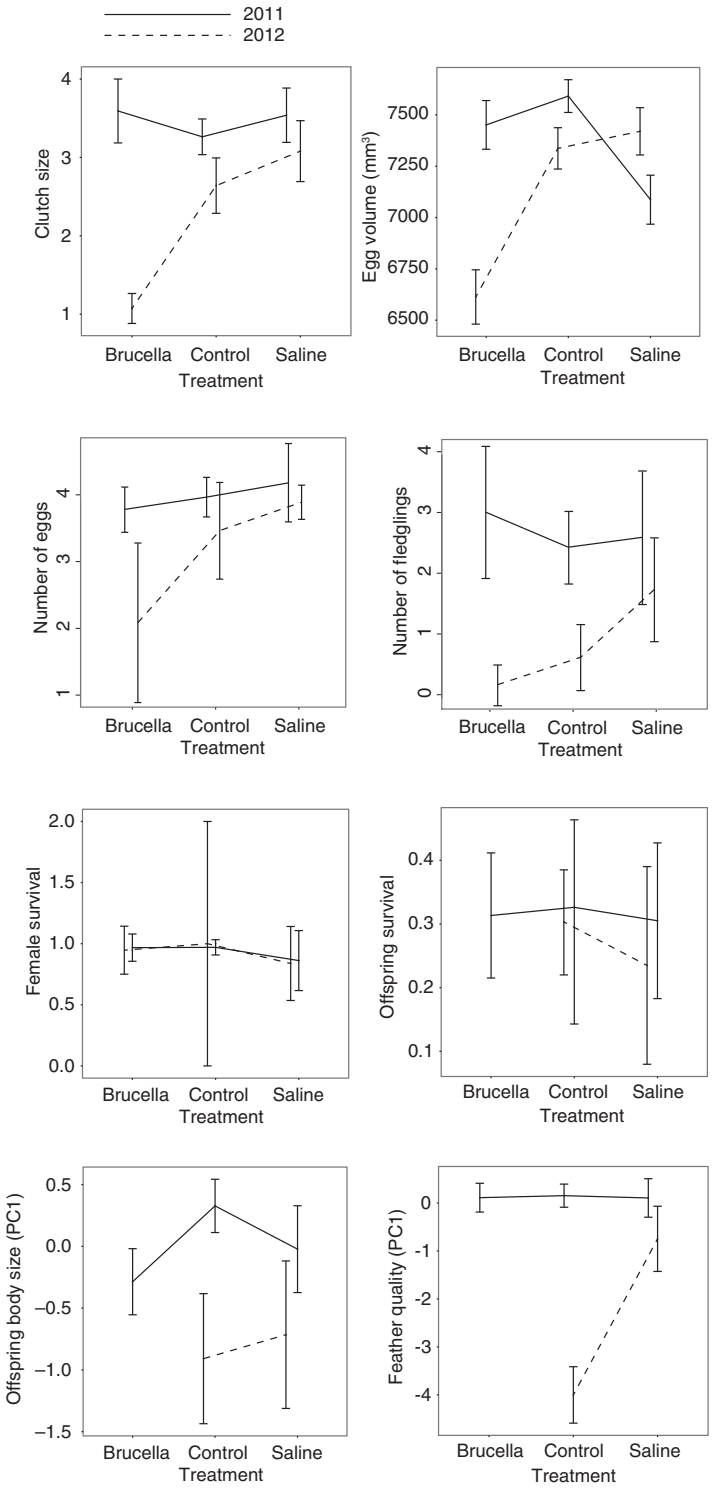

Fig. 5 Influence of *Brucella abortus* injection 2–4 weeks before egg laying on the number of eggs laid, egg volumes, offspring feather quality, offspring adult body size, as well as offspring and female survival until next year in the three treatment groups. BA injections only influenced egg volumes, reproductive allocation and offspring feather quality in 2012. No measures for offspring of BA-treated females were available in 2012 as most BA-injected females elected to skip breeding or abandoned their clutch soon after egg laying. No long-term effects on either offspring or the females were found. Note that the direction of the PC feather quality is reversed so that high values correspond to a high feather quality, meaning no fault bars. Detailed statistics are given in Table 2.

downstream costs to themselves by abandoning their nests early on, suggesting that they assessed costs of reproduction continuously.

Given the widespread occurrence of intermittent breeding in long-lived bird species (Bradley *et al.*, 2000; Covas *et al.*, 2004; Shaw & Levin, 2013), brood and clutch size manipulations provide limited insights into the consequences of reproductive decisions. Moreover, empirical studies rarely assess offspring quality or follow post-fledging survival (Santos & Nakagawa, 2012) and exclude females that exhibit intermittent breeding. Models have focused so far on the trade-off between parental survival and reproductive allocation (Hamel *et al.*, 2010), ignoring intergenerational trade-offs. Nevertheless, offspring quality is a vital contributor to fitness given that offspring need to survive and successfully reproduce (Williams, 1994). Our longitudinal and experimental data both suggest that females regulate the cost of reproduction (assessed as survival cost for females and offspring, and offspring quality) largely by adjusting the initial reproductive investment (i.e. the number of eggs laid).

Previous studies that experimentally increased costs of reproduction have reported downstream fitness consequences for females (Ardia *et al.*, 2003) or offspring (De Kogel, 1997; Krist, 2011; Santos & Nakagawa, 2012). Small egg size and/or poor early condition have negative fitness consequences for offspring in many species (Metcalfe & Monaghan, 2001; Cam & Aubry, 2011; but see Drummond *et al.*, 2011). However, most experimental studies on reproductive allocation trade-offs in birds have particularly investigated short-lived species breeding in nest boxes (Santos & Nakagawa, 2012), and manipulated birds after egg laying. Given these biases, it remains unclear whether long-lived bird species in general adjust their initial reproductive investment to produce offspring of even quality under varying environmental and body conditions, without paying a survival cost.

Studies often measure reproductive allocation at different reproductive stages (clutch or litter size vs. number of fledglings or weaned offspring), but the losses that occur between the stages differ greatly across species and across taxonomical classes. In many egg-laying species, nest predation is rampant, and thus, the difference between the number of eggs and the number of fledglings can be large, as is the case in Siberian jays. Similarly, predation and starvation of young mammals can largely increase the number of born and weaned young. Moreover, variation in individual quality (Noordwijk & Jong, 1986; Stearns, 1992) will further increase the variance of reproductive output and/or female survival. Thus, it is important to assess the changes in reproductive allocation between different stages and to specify the processes leading to a high variance of offspring quantity, facilitating future comparative work focusing on measures of reproductive allocation.

Although long-lived mammals (Hamel *et al.*, 2010) and Siberian jays both have a high variance in initial reproductive allocation but a low variance in female survival, the underlying processes are likely to differ across taxonomical classes. Long-lived mammals (i.e. species with a maximum lifespan above the mean: 16.3 years (Jones *et al.*, 2009)) require 3.6 times longer than long-lived birds (i.e. species with a maximum lifespan above the mean: 15.7 years (Valcu *et al.*, 2014)) to raise their offspring to independence (431 vs. 120 days; Drobniak *et al.*, 2015; Jones *et al.*, 2009), affecting the evolution of reproductive allocation strategies. At intermediate to high latitude, females of long-lived mammals are pregnant during winter with limited resources available, and in several long-lived mammal species, offspring experience high variance in first-year mortality (Pereira & Fairbanks, 1993; Hastings *et al.*, 1999; Gaillard *et al.*, 2000). In contrast, birds mostly breed during the time of the year when most resources are available, and are in a better position to match their reproductive allocation to the conditions during the breeding season. Thus, it would be crucial to know at which stage variance in reproductive output arises to understand the selective pressures that influence the evolution of reproductive allocation across taxonomical classes.

To conclude, our study shows that females in a long-lived bird species exhibit intermittent breeding when experiencing both harsh environmental conditions and experimentally reduced body condition. Yet, when females did commit to breeding, offspring quality (i.e. body size) did not vary between years or individuals, nor did it influence the survival of females or fledged offspring. Offspring quality has been shown to have downstream fitness effects (Lock, 2012; Burton & Metcalfe, 2014), highlighting that future life history models on reproductive allocation should consider the variance of reproductive allocation (i.e. number of eggs or litter size), reproductive output (i.e. number of fledglings or weaned offspring) and offspring quality and survival. Future long-term studies will help to determine whether other long-lived bird species also produce high-quality offspring independent of environmental or female body condition, and display a low variance of initial reproductive allocation as well as female and offspring survival.

Acknowledgments

We are grateful to Rado Kozma, Katharine Bowgen, Nicole Schneider, Jonathan Barnaby, Franzi Kurz, Chloe Swart, Jan Hildebrand and Enrico Sorato for help in the field, and three anonymous reviewers, Joanna Sendecka, Simone Webber and Carel van Schaik for helpful comments on the manuscripts. This study has been supported by grants from the Swiss National Science Foundation (MG), the Swedish Research

Council (MG, JE) and the National Science Centre, Poland, through the European Union's Horizon 2020 research and innovation programme (Marie Sklodowska-Curie grant No. 665778) (MG).

References

Amat, J., Aguilera, E. & Visser, G.H. 2007. Energetic and developmental costs of mounting an immune response in greenfinches (*Carduelis chloris*). *Ecol. Res.* **22**: 282–287.

Ardia, D.R., Schat, K.A. & Winkler, D.W. 2003. Reproductive effort reduces long-term immune function in breeding tree swallows (*Tachycineta bicolor*). *Proc. R. Soc. B Biol. Sci.* **270**: 1679–1683.

Birkhead, T., Fletcher, F. & Pellatt, E. 1998. Sexual selection in the zebra finch *Taeniopygia guttata*: Condition, sex traits and immune capacity. *Behav. Ecol. Sociobiol.* **44**: 179–191.

Bradley, J., Wooller, R. & Skira, I. 2000. Intermittent breeding in the short-tailed shearwater *Puffinus tenuirostris*. *J. Anim. Ecol.* **69**: 639–650.

Burton, T. & Metcalfe, N.B. 2014. Can environmental conditions experienced in early life influence future generations? *Proc. Biol. Sci.* **281**: 20140311.

Cam, E. & Aubry, L. 2011. Early development, recruitment and life history trajectory in long-lived birds. *J. Ornithol.* **152**: 187–201.

Clutton-Brock, T. 1991. *The Evolution of Parental Care*. Princeton University Press, Princeton, NJ.

Covas, R., Doutrelant, C. & du Plessis, M.A. 2004. Experimental evidence of a link between breeding conditions and the decision to breed or to help in a colonial cooperative bird. *Proc. R. Soc. B Biol. Sci.* **271**: 827–832.

Cubaynes, S., Doherty, P.F., Schreiber, E. & Gimenez, O. 2010. To breed or not to breed: a seabird's response to extreme climatic events. *Biol. Lett.* **7**: 303–306.

De Kogel, C. 1997. Long-term effects of brood size manipulation on morphological development and sex-specific mortality of offspring. *J. Anim. Ecol.* **66**: 167–178.

Dijkstra, C., Bult, A., Bijlsma, S., Daan, S., Meijer, T. & Zijlstra, M. 1990. Brood size manipulations in the kestrel (*Falco tinnunculus*): effects on offspring and parent survival. *J. Anim. Ecol.* **59**: 269–285.

Drobniak, S.M., Wagner, G., Mourocq, E. & Griesser, M. 2015. Family living: an overlooked but pivotal social system to understand the evolution of cooperative breeding. *Behav. Ecol.* **26**: 805–811.

Drummond, H., Rodriguez, C. & Oro, D. 2011. Natural 'poor start' does not increase mortality over the lifetime. *Proc. R. Soc. B Biol. Sci.* **278**: 3421–3427.

Eggers, S., Griesser, M., Andersson, T. & Ekman, J. 2005. Nest predation and habitat change interact to influence Siberian jay numbers. *Oikos* **111**: 150–158.

Eggers, S., Griesser, M., Nystrand, M. & Ekman, J. 2006. Predation risk induces changes in nest-site selection and clutch size in the Siberian jay. *Proc. R. Soc. B Biol. Sci.* **273**: 701–706.

Ekman, J. & Griesser, M. 2016. Siberian jays: delayed dispersal in absence of cooperative breeding. In: *Cooperative Breeding in Vertebrates: Studies of Ecology, Evolution, and Behavior* (W.D. Koenig & J. Dickinson, eds), pp. 6–18. Cambridge University Press, Cambridge.

Ekman, J., Sklepkovych, B. & Tegelström, H. 1994. Offspring retention in the Siberian jay (*Perisoreus infaustus*) - The prolonged brood care hypothesis. *Behav. Ecol.* **5**: 245–253.

Ekman, J., Eggers, S., Griesser, M. & Tegelström, H. 2001. Queuing for preferred territories: delayed dispersal of Siberian jays. *J. Anim. Ecol.* **70**: 317–324.

Ekman, J., Eggers, S. & Griesser, M. 2002. Fighting to stay: the role of sibling rivalry for delayed dispersal. *Anim. Behav.* **64**: 453–459.

Erikstad, K.E., Fauchald, P., Tveraa, T. & Steen, H. 1998. On the cost of reproduction in long-lived birds: the influence of environmental variability. *Ecology* **79**: 1781–1788.

Fontaine, J.J. & Martin, T.E. 2006. Parent birds assess nest predation risk and adjust their reproductive strategies. *Ecol. Lett.* **9**: 428–434.

Gaillard, J.-M., Festa-Bianchet, M., Yoccoz, N., Loison, A. & Toigo, C. 2000. Temporal variation in fitness components and population dynamics of large herbivores. *Annu. Rev. Ecol. Syst.* **31**: 367–393.

Gasparini, J., Boulinier, T., Gill, V., Gil, D., Hatch, S. & Roulin, A. 2007. Food availability affects the maternal transfer of androgens and antibodies into eggs of a colonial seabird. *J. Evol. Biol.* **20**: 874–880.

Gilmour, A.R., Gogel, B., Cullis, B., Thompson, R. & Butler, D. 2009. *ASReml User Guide Release 3.0*. VSN International Ltd, Hemel Hempstead, UK.

Gorman, H.E. & Nager, R.G. 2004. Prenatal developmental conditions have long–term effects on offspring fecundity. *Proc. R. Soc. Lond. B Biol. Sci.* **271**: 1923–1928.

Grant, P.R., Grant, B.R., Keller, L.F. & Petren, K. 2000. Effects of El Niño events on Darwin's finch productivity. *Ecology* **81**: 2442–2457.

Griesser, M. 2003. Nepotistic vigilance behavior in Siberian jay parents. *Behav. Ecol.* **14**: 246–250.

Griesser, M. 2013. Do warning calls boost survival of signal recipients? Evidence from a field experiment in a group-living bird species. *Front. Zool.* **10**: 49.

Griesser, M., Nystrand, M. & Ekman, J. 2006. Reduced mortality selects for family cohesion in a social species. *Proc. R. Soc. B Biol. Sci.* **273**: 1881–1886.

Griesser, M., Nystrand, M., Eggers, S. & Ekman, J. 2007. Impact of forestry practices on fitness correlates and population productivity in an open-nesting bird species. *Conserv. Biol.* **21**: 767–774.

Griesser, M., Nystrand, M., Eggers, S. & Ekman, J. 2008. Social constraints limit dispersal and settlement decisions in a group-living bird species. *Behav. Ecol.* **19**: 317–324.

Griesser, M., Schneider, N.A., Collis, M.-A., Overs, A., Guppy, M., Guppy, S. *et al.* 2012. Causes of ring-related leg injuries in birds – evidence and recommendations from four field studies. *PLoS ONE* **7**: e51891.

Griesser, M., Halvarsson, P., Sahlman, T. & Ekman, J. 2014. What are the strengths and limitations of direct and indirect assessment of dispersal? Insights from a long-term field study in a group-living bird species. *Behav. Ecol. Sociobiol.* **68**: 485–497.

Griesser, M., Halvarsson, P., Drobniak, S.M. & Vila, C. 2015. Fine-scale kin recognition in the absence of social cues in the Siberian jay, a monogamous bird species. *Mol. Ecol.* **24**: 5726–5738.

Griffiths, R., Double, M.C., Orr, K. & Dawson, R.J.G. 1998. A DNA test to sex most birds. *Mol. Ecol.* **7**: 1071–1075.

Grubb, T.C. 2006. *Ptilochronology. Feather Time and the Biology of Birds*. Oxford University Press, Oxford.
Hamel, S., Gaillard, J.-M., Yoccoz, N.G., Loison, A., Bonenfant, C. & Descamps, S. 2010. Fitness costs of reproduction depend on life speed: empirical evidence from mammalian populations. *Ecol. Lett.* **13**: 915–935.
Hastings, K., Testa, J. & Rexstad, E. 1999. Interannual variation in survival of juvenile Weddell seals (*Leptonychotes weddellii*) from McMurdo Sound, Antarctica: effects of cohort, sex and age. *J. Zool.* **248**: 307–323.
Hoyt, D.F. 1979. Practical methods of estimating volume and fresh weight of bird eggs. *Auk* **96**: 73–77.
Jones, K.E., Bielby, J., Cardillo, M., Fritz, S.A., O'Dell, J., Orme, C.D.L. *et al.* 2009. PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals: Ecological Archives E090-184. *Ecology* **90**: 2648–2648.
Karell, P., Kontiainen, P., Pietiäinen, H., Siitari, H. & Brommer, J. 2008. Maternal effects on offspring Igs and egg size in relation to natural and experimentally improved food supply. *Funct. Ecol.* **22**: 682–690.
Kerr, T.D., Boutin, S., LaMontagne, J.M., McAdam, A.G. & Humphries, M.M. 2007. Persistent maternal effects on juvenile survival in North American red squirrels. *Biol. Lett.* **3**: 289–291.
Krist, M. 2011. Egg size and offspring quality: a meta-analysis in birds. *Biol. Rev.* **86**: 692–716.
Lock, J.E. 2012. Transgenerational effects of parent and grandparent gender on offspring development in a biparental beetle species. *Biol. Lett.* **8**: 408–411.
Metcalfe, N.B. & Monaghan, P. 2001. Compensation for a bad start: grow now, pay later? *Trends Ecol. Evol.* **16**: 254–260.
Mourocq, E., Bize, P., Bouwhuis, S., Bradley, R., Charmantier, A., de la Cruz, A. *et al.* 2016. Lifespan and reproductive costs explain interspecific variation in the optimal onset of reproduction. *Evolution* **70**: 296–313.
Noordwijk, A.J.V. & Jong, G.D. 1986. Acquisition and allocation of resources: their influence on variation in life history tactics. *Am. Nat.* **128**: 137–142.
Nystrand, M., Griesser, M., Eggers, S. & Ekman, J. 2010. Habitat-specific demography and source-sink dynamics in a population of Siberian jays. *J. Anim. Ecol.* **79**: 266–274.
Pardo, D., Barbraud, C. & Weimerskirch, H. 2014. What shall I do now? State-dependent variations of life-history traits with aging in Wandering Albatrosses. *Ecol. Evol.* **4**: 474–487.
Parejo, D., Avilés, J. & Rodríguez, J. 2012. Supplemental food affects egg size but not hatching asynchrony in rollers. *Behav. Ecol. Sociobiol.* **66**: 1097–1105.
Pereira, M.E. & Fairbanks, L.A. 1993. *Juvenile Primates: Life History, Development and Behavior*. University of Chicago Press, Chicago, IL.
Robinson, M.R., Wilson, A.J., Pilkington, J.G., Clutton-Brock, T.H., Pemberton, J.M. & Kruuk, L.E. 2009. The impact of environmental heterogeneity on genetic architecture in a wild population of Soay sheep. *Genetics* **181**: 1639–1648.
Roff, D.A. 1992. *The Evolution of Life Histories*. Chapman and Hall, New York, NY.
Santos, E.S.A. & Nakagawa, S. 2012. The costs of parental care: a meta-analysis of the trade-off between parental effort and survival in birds. *J. Evol. Biol.* **25**: 1911–1917.
Shaw, A.K. & Levin, S.A. 2013. The evolution of intermittent breeding. *J. Math. Biol.* **66**: 685–703.
Sild, E., Sepp, T., Männiste, M. & Hõrak, P. 2011. Carotenoid intake does not affect immune-stimulated oxidative burst in greenfinches. *J. Exp. Biol.* **214**: 3467–3473.
Stearns, C.C. 1992. *The Evolution of Life Histories*. Oxford University Press, Oxford.
Stinchcombe, J.R., Kirkpatrick, M. 2012. Genetics and evolution of function-valued traits: understanding environmentally responsive phenotypes. *Trends Ecol. Evol.* **27**: 637–647.
Team, R. C. (2014) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. 2013. pp. ISBN 3-900051-07-0.
Valcu, M., Dale, J., Griesser, M., Nakagawa, S. & Kempenaers, B. 2014. Global gradients of avian longevity support the classic evolutionary theory of ageing. *Ecography* **37**: 930–938.
Williams, G.C. 1966. Natural selection costs of reproduction and a refinement of lacks principle. *Am. Nat.* **100**: 687–690.
Williams, T.D. 1994. Intraspecific variation in egg size and egg composition in birds: effects on offspring fitness. *Biol. Rev.* **69**: 35–59.
Williams, T.D. 2001. Experimental manipulation of female reproduction reveals an intraspecific egg size clutch size trade-off. *Proc. R. Soc. Lond. B Biol. Sci.* **268**: 423–428.
Williams, E.V. & Swaddle, J.P. 2003. Moult, flight performance and wingbeat kinematics during take-off in European starlings *Sturnus vulgaris*. *J. Avian Biol.* **34**: 371–378.

Supporting information

Additional Supporting Information may be found online in the supporting information tab for this article:
Table S1 Overview of the number of Siberian jay females involved in experimental treatments.
Table S2 Generalized linear mixed models assessing the influence of experimental treatment in the first year on the reproductive investment and female survival in the second year ($n = 15$ females that were injected repeatedly).
Table S3 Principal component analyses of offspring body size (a) and feather quality (b).
Table S4 Random part of repeated measurement regression (Table 2, Model a).
Data S1 Simulation to test for the link between average clutch size and the proportion of successfully breeding females.

Data deposited at Dryad: doi: 10.5061/dryad.755jp

Received 2 May 2016; revised 18 January 2017; accepted 24 January 2017